ON THE TAXONOMY, ECOLOGY AND PHYSIOLOGY OF A GIANT OYSTER, *CRASSOSTREA PARAIBANENSIS*, NEW SPECIES

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ABSTRACT

A new large species of the Brazilian oyster, *Crassostrea paraibanensis* is described and compared with some closely related members of the genus *Crassostrea*. This new species is the largest of its kind, and, despite some similarities, it differs from all other species of *Crassostrea*. The ecology of the localities of this economically important species is described, together with aspects of its physiology, ecology and culture methods.

During recent ecological surveys of estuaries, particularly the confines of the large river mouths of Paraiba, many commercially important bony fishes, crustaceans and mollusks were found. In common with many other species in this habitat, I found a new species of giant oyster, which appears to be endemic and confined to the northeastern part of Brazil. The present work commenced in September, 1976, with the idea that this oyster was *Crassostrea brasiliana*. However, based on additional information of the biology, physiological behavior and culture, it became apparent that this form differs in many respects not only from *Crassostrea brasiliana* as originally described by Lamarck (1819), but also from all other known species of the genus *Crassostrea*. This paper reports the taxonomic, ecological and some physiological aspects of this new species.

MATERIALS AND METHODS

Samples were collected by diving on two oyster sites of the Paraiba River estuary (Fig. 1). Body dimensions, shell cavity volume, and wet and dry weights were determined to the nearest millimeter and milligram respectively. Dry weights were determined by drying at 68°C in a thermostatically controlled oven until two consecutive weighings were consistent. Abiotic factors such as salinity, temperature, pH and turbidity were determined biweekly, for a period of 2 years. Larvae were isolated from plankton samples obtained at the oyster sites, and also eggs were hatched out and larvae reared in glass aquarium tanks in the laboratory using filtered estuarine water collected from the same oyster beds. Soft parts were examined by dissecting fresh specimens and specimens preserved in a mixture of 4% neutral formaldehyde and 70% alcohol. Photographs were made from life; drawings of the larvae and the ligament above the hinge axis were made with the help of a camera lucida attached to a monocular microscope.

HISTORICAL TAXONOMIC REVIEW

The systematic position of oysters of Brazil is rather ambiguous and far from complete. Archaeological studies using radiocarbon dating (Fairbridge, 1976) suggest that the principal food of the Indians, who settled along the coastal belts and estuaries of Brazil during the Holocene, about 7,000 years ago, consisted of oysters such as *Ostrea brasiliana, Ostrea arborea* and other large species.

The new species is thoroughly described because of the past confusion. In my extensive surveys and close examinations of oysters, including ones from other countries, such as *Crassostrea angulata, C. virginica, C. gigas* and *C. cucullata,* I have found, besides *Ostrea cristata* Born, 1778, at least three very distinct indigenous species of the genus *Crassostrea* in Brazil. These include *Crassostrea paraibanensis,* new species described herein; the closely allied *C. brasiliana*
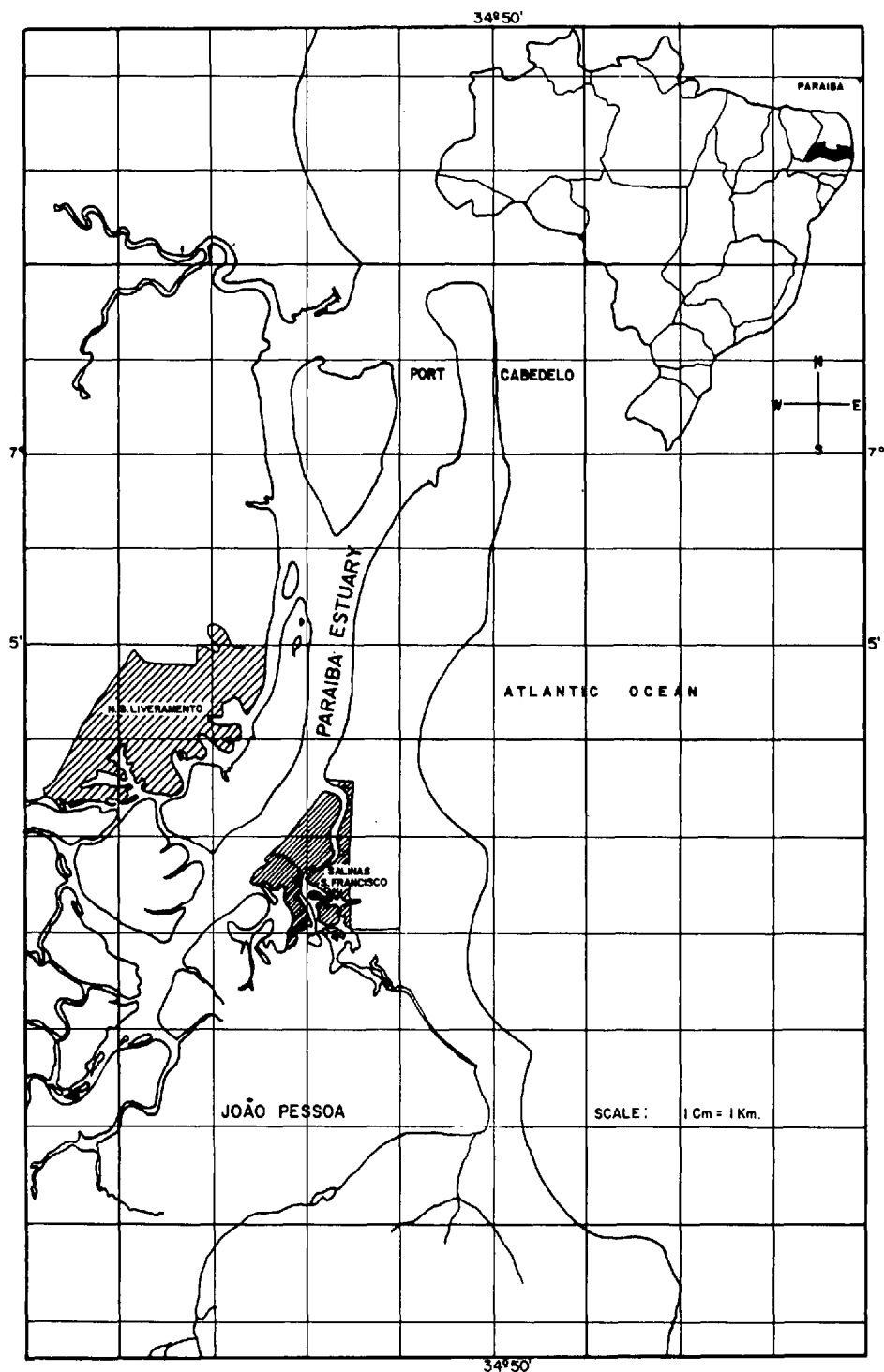
Figure 1.   The commercial oyster culturing sites of Salinas and Livramento which are located on the two main arms of Paraiba River estuary. Map of Brazil (insert) showing Paraiba State, not drawn to scale.

Lamarck, 1819 and a third unknown species *C. sp. C. brasiliana* has been included often under the names *Crassostrea rhizophorae* Guilding, 1828; *Ostrea rhizophorae* (Mattox, 1949) and *Ostrea arborea* (Lima et al., 1963; Antunes et al., 1968; Fairbridge, 1976; H. S. Lopes, personal communication). In my opinion, *Crassostrea rhizophorae, O. arborea* and *Crassostrea (O.) brasiliana* are identical and hence synonyms, but *Crassostrea paraibanensis* is a separate species, and quite different from others, though previously confused with and still locally being called *Crassostrea brasiliana*.

The original description of Lamarck (1819) is as follows: "11. Oyster from Brazil. *Ostrea brasiliana* Lamk. (3) Shell delicate, oval, dilated, fulvous white subradiate; transverse striations extremely fine. Habitat: the coast of Brazil. Mus. No. De Lalande. Small size, superior valve slightly convex."

Lamy (1929) saw the type which Lamarck preserved in the Paris Museum, brought by De Lalande from Brazil. Although Lamy gave approximate measurements of the type, he made no attempt to redescribe them. His measurements of the types are: two small specimens: 22 × 18 mm and 17 × 16 mm and these were fixed inside another slightly larger 43 × 29 mm inferior valve. These were considered by Deshayes (1836) as a variety of *Ostrea borealis*, but Ihering (1907) admitted it to be a synonym of *Ostrea rhizophorae*.

The description by Lamarck of *Crassostrea brasiliana* fully agrees with the structure of small specimens of *Crassostrea rhizophorae*, but I am not convinced that the specimens described by Lamarck and the subsequent local workers and the one described here as a new species are one and the same.

I have examined the original type specimens of *Crassostrea brasiliana* of Lamarck which I obtained from the Paris Museum and give the following brief account of the type specimens of *C. brasiliana* for comparison.

These consisted of two smaller specimens fixed firmly to the inner surface of a slightly bigger left valve (Fig. 4). The two smaller specimens, probably of the same generation, are foliaceous, but they slightly differ in size. They have the following dimensions: H 22 × L 18 × W 3.5 mm and H 18 × L 15 × W 3 mm respectively. Their right valves are thin and flat and well fitting to the left valves. The beaks of the left valves are short and slightly grooved, as seen under a binocular microscope, while the beaks of the right valves are very much reduced. The muscle scars are kidney shaped or round, purplish in color, especially in the slightly larger one of the two.

The left valve which forms the substrate for the above two smaller oysters is more certainly of an older generation. It is relatively bigger (H 38.5 × L 28 × 0.5 W 6 mm, the 0.5 width being measured as the maximum distance between the convex surface and the sagittal plane), foliaceous and relatively shallower. The resilium, about 5 mm long, slightly arched ventrally and still attached at each end to the tensila, is remarkably intact. The groove of the beak appears fully covered by the buttress, split lengthwise along its median axis, and consequently the retention of the resilium and tensila on the left valve. The adductor muscle scar is slightly distorted by erosion and a small perforation, but the color still appears somewhat purplish. The outer convex surface is also eroded but otherwise fairly smooth and tawny or pale brown in color with its summit subcircular and flattened out thus showing clearly the point of attachment to the substrate. More than 20 tiny barnacles still remain settled on the outer surface of this valve while one is attached to the surface between the tip of the beak and the center of the resilium.

Because of the lack of any previous description and the general discrepancies, in particular in the size of oysters, the diagnostic characters of *Crassostrea par-*
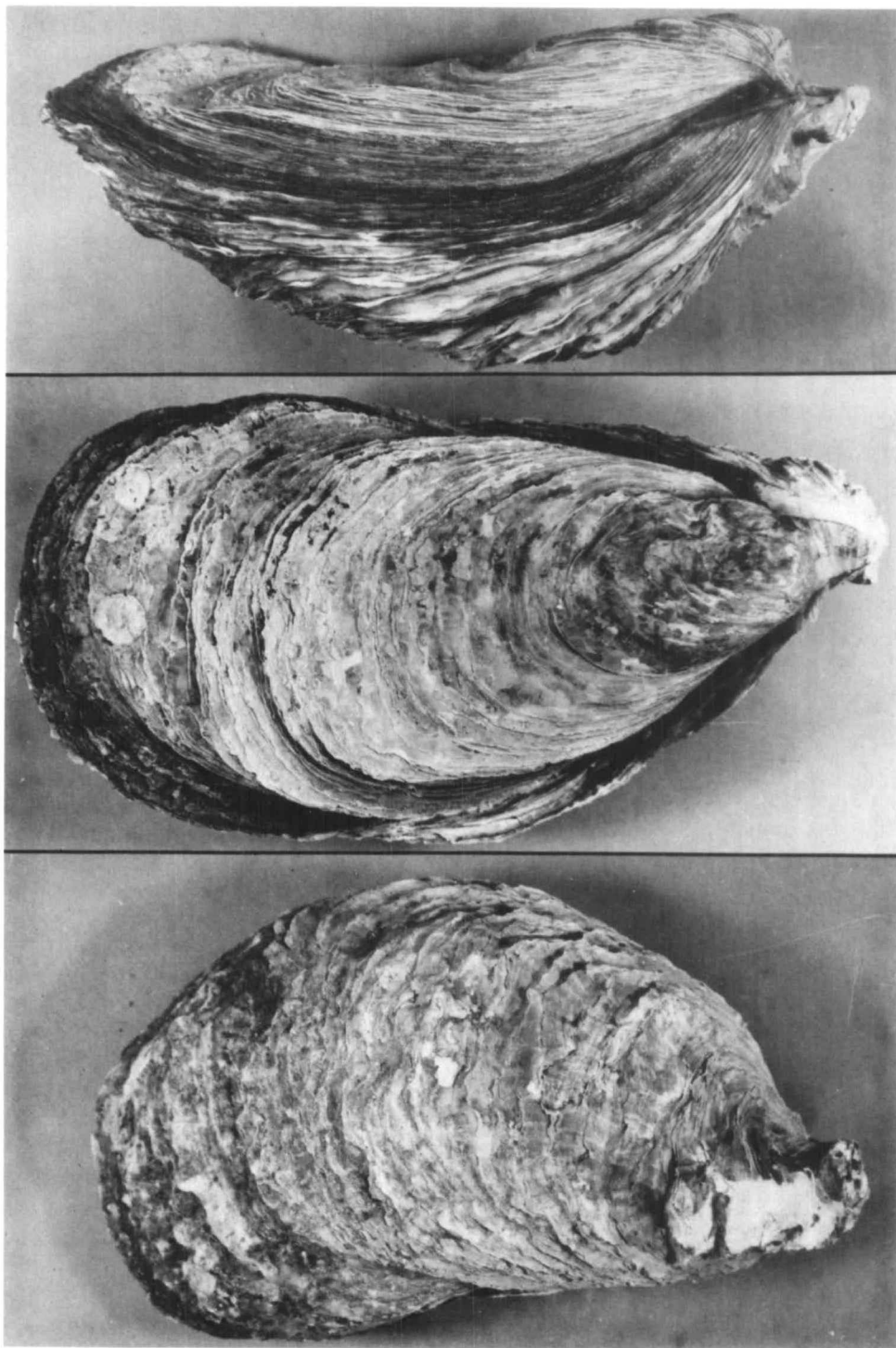
Figure 2. (*Upper*) *Crassostrea paraibanensis* new species in its natural position, lateral view, with the right shallow valve up and the deeply cupped left valve down. Lamellated eccentric rings are clearly visible on both valves. Actual life size: height 206 × length 96 × width 72 mm and weighing 1,005 g whole weight. The specimen was collected from Salinas estuary at 2.8 m depth. All photo-

Figure 3. *Crassostrea paraibanensis* with right valve removed by breaking the ligament along the hinge axis and by carefully cutting the adductor muscle so as to expose the mantle contents retained in the deeply cupped left valve. The muscle scar is distinctly seen on the inside white glossy surface of the right valve. The specimen, actual life size: 182 × 100 × 80 mm and weighing 1,150 g whole weight, was collected from Livramento estuary at 2.2 m depth.

aibanensis, together with a brief review of the distinguishing features of the two closely related species found in Brazil, should be very useful.

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Superfamily OSTREACEA Rafinesque, 1815
Family OSTREIDAE Rafinesque, 1815
Subfamily OSTREIDAE Rafinesque, 1815
Genus *CRASSOSTREA* Sacco, 1897

Crassostrea paraibanensis new species
Figures 2 and 3

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Type Locality and Habitat.—This oyster has been found in two locations, Salinas and Livramento, the two principal natural oyster beds of Paraiba River estuary (Fig. 1) and appears to be endemic and confined to the northeastern part of Brazil. These oysters prefer soft muddy bottom, well below tide mark.

←

graphs are by electronic flash, except Figs. 5 and 6. (*Middle*) The same specimen as in Fig. 2 viewed from above, showing the straight beak from the ventral valve. The eccentric lamellated rings are seen on the outer surface of the right valve. (*Lower*) The same specimen as in Figs. 2 and 3, viewed from below. The white patch on the surface of the ventral valve near the umbo or dorsal end showing slight damage caused by separation of the oyster from a small rocky substratum to which it was attached. The eccentric lamellated rings are also seen on the outer surface of the left valve.

Type Material.—Holotype: British Museum (Natural History), Reg. No. 1978114, 206 × 96 × 72 mm; 1,005 g; Paratypes: BM(NH), 1978115, 210 × 110 × 70 mm; 958 g; and Rio de Janeiro National Museum, 3815, 250 × 110 × 90 mm; 1,108 g; and RJNM, 3816, 220 × 110 × 75 mm; 1,036 g.

Diagnosis.—Shell large, both valves very thick and outer surfaces lamellated, left valve deeply cupped and right valve very shallow to nearly flat; beak with deep furrow and with cross ripple marks; resilium longitudinally and transversely striated. Rectum tubular with an abrupt constriction at the proximal end. Prodissoconch hinge short and straight and crenulations indistinct at each end of the hinge axis.

Description.—Shell variable in size and outline; adult two- to four-year old specimens elongated with ventral valve margin very broad, nonundulating and fairly smooth, thin, but somewhat brittle. Shell very thick and strong elsewhere. In fresh condition, outer surface of shell usually coarse and towards ventral margin color dark gray, changing to pale brown gradually towards the umbo. Valves asymmetrical and unequal; right (upper) valve slightly smaller, fitting very tightly. Left (lower) valve large and deeply cupped with strong clearly extended, usually straight beak with pronounced resilifer (furrow). Right valve flat or relatively shallow except for a small depression on inner surface which probably accommodates bulging digestive diverticulum and promyal chamber, and generally about beak's length shorter than left valve. Beak usually reduced, but when present, its furrow replaced by low buttress, curving back towards hinge, posterior to ventral beak (Fig. 2).

Shells usually lack convoluted, plicated, or fluted sculpture; the valve surfaces coarse showing well defined eccentric, very closely packed, extremely thin, lamellated rings, commencing from umbo-end. Three- to four-year individuals, each valve consists of an average of 84 rings. Rings more easily seen along commissural plane or median lateral side where two valves form deep groove on either side when tightly closed. Young oysters less than two years old have nearly round or slightly elongated shells and lamellated rings reduced or absent.

Inner surface of shells smooth, milky white and glossy, except at adductor muscle scar. Rarely irregularly shaped small patches of "chalky deposits" seen, especially in older oysters. Between external and internal surfaces of shell a thick, compact layer of chalky material.

Hinge edentulous, and adult hinge probably replaced by resilium along the hinge axis. Ligament dorsal, outside cardinal plateau, strong deep gray in color, covering resilium and tensila, but greater part of ligament spreads out externally on the shell and oldest part becomes disintegrated towards beak ends, leaving only some sand-like particles.

Resilium almost extends into shell cavity, particularly when valve recessed below, thus resilium neatly fits into resilifer or chondrophore of left beak; two ends of resilium attached to suspensory-ligament-like tensila. In adult oysters, resilium is about 18–24 mm long and 2 mm thick. Resilium, together with tensila, and surrounding ligament separate with right valve. Resilium, when examined under binocular microscope, consists of about 4–6 bands arranged parallel to one another along longitudinal axis; all but one, or seldom two, striated both in longitudinal and transverse directions. Inner growing margin nonstriated, smooth and creamy in color; then followed by striated bands, displaying a variety of hues such as brown, orange, pink, violet, blue and gray in ventrodorsal direction. Transverse ripply marks generally gray and glossy, and often too hard, and might reflect difference in composition. External surface of resilium lined by thin layer of gray ligament. Nonstriated layer or band, when present, probably represents

noncalcified matrix. Tensila also cross-striated but always glossy and gray. Pro-dissoconch hinge short and straight and crenulations indistinct at each end.

Anatomy.—Adductor muscle (Fig. 3) the most conspicuous part and relatively short and very stout, crossing whole width of the body. At each end inserted firmly on the inner surface of the valves; richly supplied with blood vessels and nerve fibers.

Muscle scar (imprint) farther removed from hinge end and usually located little toward ventral end from center of valve. Size and shape of muscle fairly constant, nearly comma shaped or like combination of half-kidney and half-crescent with sharp curve pointing dorsally, close to posterior margin of the valves; usually brown in color.

Quenstead muscle (Stenzel, 1971, assumes to be present in all oysters) hardly visible, fine point of attachment located between mantle membrane covering center of digestive diverticulum and shell, about 2–3 cm from center of hinge axis. (Clearly marked out areas around attachments, when examined under binocular microscope, show no discernible imprint of Quenstead muscle because point of attachment is so fine and superficial that it gets easily detached from surface of valve while opening the shell).

Promyal chamber (Kellogg, 1892; Nelson, 1938) asymmetrical space lying only on right side between visceral mass and right mantle or pallium. Careful examination by cutting across adductor muscle more towards right side revealed extremely thin membrane which adheres to visceral mass, together with transparent pericardial membrane which delimits it ventrally, actually separates the promyal chamber from visceral mass itself. Right mantle partly fused around convex aspect of laterally compressed disc-like digestive diverticulum, dorsally and also around adductor muscle, ventrally. Promyal chamber continuous from dorsal end, below attachment of right mantle to diverticular region, with epibranchial chamber and cloaca ventrally, running between adductor muscle and curved basal plate of water tubes. Posterior margin of mantle lobes mostly free, except at dorsoposterior end where fused, above labial pulps, forming ∧-shaped groove which continues above arch of digestive diverticulum for short while and leads into promyal chamber. Toward ventroposterior end, mantle membranes fuse above cloaca with tip of gills to form palliobranchial junction. Basal girdle-like plate perforated by four rows of water tubes which communicate with gills. Each row consists of 36 water tubes; 10 confined to promyal part while remaining 26 seen from beneath adductor muscle, epibranchial chamber and cloacal part combined. Tubes in cloacal region, below palliobranchial fusion, extremely small and visible only with some difficulty.

Two paired gills slightly arched and covered by mantle lobes and outer margins run parallel to mantle margins. Gill ends fused anterodorsally just behind labial pulps and partly covered by them, and posteroventrally at palliobranchial junction. Color of the gills often changes depending on amount of mucus secreted and quality of water that they filter, sometimes appear greenish when diatoms available in abundance.

The heart consists of two auricles and single ventricle. Auricles darker in color than ventricle. Blood emptied into bulbous sinus venosus and pumped into the aorta by muscular ventricle. Blood vessels supplying the adductor muscle, visceral mass and mantle lobes quite conspicuous.

Kidneys (organs of Bojanas) visible between auricles and intestinal loop as tiny pigmented tubules which open into cloacal passage close to genital aperture.

Visceral mass occupies relatively large space between dorsal and adductor

muscle. Alimentary tract includes narrow slit like mouth which lies between hood formed by fusion of mantle folds and two pairs of labial pulps at dorsal end of gills. Mouth leads into relatively short esophagus which, in turn, opens into large stomach; the latter also receives profusely branched digestive diverticulum-glandular and usually greenish in color. Intestine extends little beyond anteroventral aspect of adductor muscle, running adjacent to heart but does not pierce through it, and reflects back forming a loop and then encircles digestive diverticulum; continues further, by crossing loop, to posterior side of adductor muscle where it abruptly constricts to form relatively short and narrow rectum. Rectum ends in slit-like anus opening into cloacal passage.

Gonads conspicuous only during the sexual maturity and extend from digestive diverticulum to adductor muscle. Sexes separate; when matured, male spermary appears faintly bluish while ovaries appear yellowish to brownish in color.

Nervous system consists of principally two paired ganglia and two connectives and their derivatives. Visceral ganglion, formed by fusion of right and left ganglia, closely attached to anteroventral surface of adductor muscle and easily visible, giving rise to several nerves which control adductor muscle, visceral organs, gills and mantle lobes. Pair of connectives run along anterior ridge, buried in connective tissue, of the visceral mass and link with cerebral ganglion which lies at base of labial pulps proximal to mouth. Cerebral ganglion also formed by fusion of two ganglia of larval stage; innervates mainly four labial pulps and region around mouth. Cerebral ganglion seen only with some difficulty. Nerves and ganglia in fresh condition are whitish in color but preserved specimens facilitate dissection greatly and nervous tissue appears yellowish and relatively easy to recognize.

Physiology and Behavior.—Field observations and laboratory experiments confirmed that, during feeding, the valves open only slightly, not exceeding 2–6 mm wide between the broad ventral valve margins, and the gap diminishes rapidly towards dorsal end. The opening or closure, the former a very gradual and the latter an abrupt movement, is brought about by the right valve only and is regulated by the neuromuscular mechanism. The adductor muscle responds quite rapidly to the slightest changes in the environment by quick contraction and by closing the valves. When oysters are removed from the water, the adductor muscle remains continuously contracted and the valves closed watertight, thus helping the oysters to retain sufficient water so that they can be kept alive for more than 3 days; the spat more viable than adults. On the contrary, the muscle relaxes slowly during opening of the valves, and may sustain the position for a long period of time.

Rough estimates have shown that the adult promyal chamber can contain an average of 10 ml of water. The promyal chamber and the gills obviously communicate through the water tubes, thus suggesting some respiratory function though functions such as cleansing (Nelson, 1938) and sperm discharge (Galtsoff, 1964) have been suggested.

The gill filaments covered by numerous powerful cilia continue to beat even after isolation of tissues, thus they appear to function independently of the nervous control.

In situ experiments on heart have shown that the blood circulation, in an oscillatory manner, is effectively maintained by the rhythmic contraction and relaxation of the heart. The heart beat continues for more than 2 hours even after removal of both valves. The rate of rhythmic movement of the heart and surging of blood were further observed with "super 8 cinefilms."

Laboratory estimates have shown that a single female can produce over

29,000,000 eggs per spawning. When observed, under binocular microscope, the eggs are liberated in large numbers, enmeshed in small squirts of mucus which the oysters release intermittently and the whole process appeared to be completed within an hour. The eggs are small and about 47 μm in diameter. The females are nonincubatory and fertilization is external, and sex reversal has not been observed.

The average spawning temperature and salinity had been observed to be 29.59°C and 17.50‰ respectively. However, the peak spawning curiously coincides with the heavy rainfall when temperature remains fairly constant, though salinity becomes considerably reduced. Perhaps, the sudden drop in salinity might act as a spawning stimulus for these oysters.

During spawning time, the guts were relatively empty though the contents of the normally well fed oysters consisted of a variety of both planktonic and benthic diatoms, ciliates, tintinnids, nauplii larvae of cirripeds and copepods, besides inorganic and organic detritus.

Faecal materials were observed to be ejected forcibly along the excurrent to a distance of more than 6 cm, in a continuous stream from the ventral margin close to palliobranchial fusion, probably by the concomitant contraction of the adductor muscle and the pallial walls of the epibranchial chamber and cloacal passage. The faecal contents generally consisted of a shiny ash-like substance, including undigested diatom frustules of centrale type.

Adult oysters when subjected to changes of hydrostatic pressure, particularly in a manner described earlier (Singarajah, 1966) and such experiments were carried out to coincide with a time of high tide on a full moon day with a tidal range of 2.4 m, showed no response of any kind and a lunar periodicity was distinctly absent though a relationship between spawning and lunar periodicity had been shown in other species (Orton, 1926; Korringa, 1947; Eisawy, 1974). On the other hand, the straight hinged and pediveliger larvae responded readily to changes in pressure equivalent to 2.5 m of sea water by increased activity and generally upward swimming and to decrease in pressure by passive peculiar rotatory swimming with decreased activity, sinking under gravity.

Ecology.—The topographical and hydrological conditions of the estuaries have already been reported elsewhere (Singarajah, 1978). Only a very brief account of the oyster growing sites will be considered here. The shellfish farms at Salinas and Livramento estuaries (Fig. 1) are small bay-like sheltered inlets, which are separated from each other by about 3.5 km. Some 1272 ha (1 ha = 2.471 acres) are under cultivation. These two sites are in close proximity to the main estuary of Cabedelo Port, and the tidal ranges in the area are not great enough to cause any drastic differences in salinities.

The natural oyster beds, fringed by mangrove swamps, are typically estuarine, with soft evenly formed muddy bottoms, and remain completely submerged, even at low tide. Tides fluctuate between one and little over two meters and the water depth ranges from 3 to 3.5 m. The bottoms generally lack any hard substrate, except for incrustations formed by settlement of oysters and artificially provided substrates, and in some areas sandstones break through the mud. Apart from these, a few mangrove trees generally support a dense population of oysters. Some planted wooded poles are covered, below the high water level, with fouling organisms such as barnacles and *Sertularia,* competing with oyster spat for both food and space. Frequently, the fine lamellated sculpture of the shell of *C. paraibanensis* forms the natural abodes for the gammarid amphipod, *Ampelisca brevisimulata* which appears to be a potential pest on this oyster. The intertidal zone

of both banks of the main estuary is a mud flat, followed by low mangrove bushes of *Avicennia tomentosa* and then high mangrove trees, especially *Laguncularia racemosa* and *Rhizophora mangle* with multiple stilt roots.

The temperature range for the two oyster sites of Salinas and Livramento was 25° to 29.8° (Mean 27.9°C), and 25° to 30°C (Mean 28°C) respectively; and the salinity range for the corresponding sites was 5.20 to 22.60‰ (mean 18.20‰), 2.50 to 22.40‰ (Mean 16.80‰). The total suspended material also varies quite considerably, ranging from 20 mg/l to 118.2 mg/l. The strong trade winds coupled with tidal currents, especially during torrential tropical rainfall, contribute largely to the turbidity of the water. Measurements of transparency, using a Secchi disc, at the two sites ranged from 0.32 to 0.40 m and 0.30 to 0.40 m respectively; the low light penetration might largely be due to high turbidity. The pH was recorded only in the surface waters of the two sites and ranged from 6.40 to 7.80 and 6.20 to 7.0 and the relatively low pH might again be correlated with turbidity, the occurrence of detrital materials, increased solar radiation and other effluents of terrestrial and fresh water origin.

The concentration of dissolved oxygen, by Winkler method, also varied at the two sites from 3.21 to 6.25 and 2.12 to 5.52 ml/l respectively, and the concentration of oxygen was generally low, particularly during low tide.

Routine analyses of plankton samples collected from both oyster sites showed quantitative rather than qualitative differences. Most species were identified and quantitative estimates showed that these estuaries were far more productive than expected. Densities of plankton in both sites varied enormously, ranging from 680,000 to 7,000,000 per liter at Salinas and 480,000 to 5,000,000 per liter at Livramento respectively and ciliates, dinoflagellates and diatoms, especially were the most abundant.

The quantitative and qualitative difference of plankton between the two sites might be due to the fact that though the two estuaries are linked by the tidal currents, the close proximity of Salinas to the main channel enables it to receive more plankton directly from the inshore waters. Samples obtained from the sea water confirmed this since most of the species collected from Salinas estuary were identical to those of the marine environment, except for the consistent occurrence of *Gyrosigma* sp.

In addition to oysters, these estuaries produce a great variety of marine products, including edible fishes, particularly *Mugil brasiliensis*, shrimps, and crabs.

Prodissoconch.—The prodissoconch of *Crassostrea paraibanensis* is not easily distinguished from that of *Crassostrea brasiliana* as both larvae spend a part of their early life in free swimming planktonic form, though they can be easily seen under the microscope. In the early D-veliger stage, the larvae of both species are straight-hinged and small, less than 130 μm in length. However, the fully grown pediveliger larvae are recognizable on the basis of well defined umbo (Fig. 5), comparatively large size (240–312 μm between umbo and the opposite margin) and by the presence of long and powerful cilia which protrude from the velum between the tiny shells. These features, particularly the umbo, are somewhat reduced in *Crassostrea brasiliana* of the corresponding stage. Ranson (1948; 1960) attempted to identify oysters on the basis of well developed (umbone) prodissoconchs, and gave a figure of *C. rhizophorae* which agrees somewhat with *C. brasiliana* and not with *Crassostrea paraibanensis*. It is of interest that, occasionally, the basic pattern of the nervous system, especially the visceral and cerebral ganglia and the two connectives, can be seen in the pediveliger larvae of *Crassostrea paraibanensis*. Furthermore, observations on spat reared under
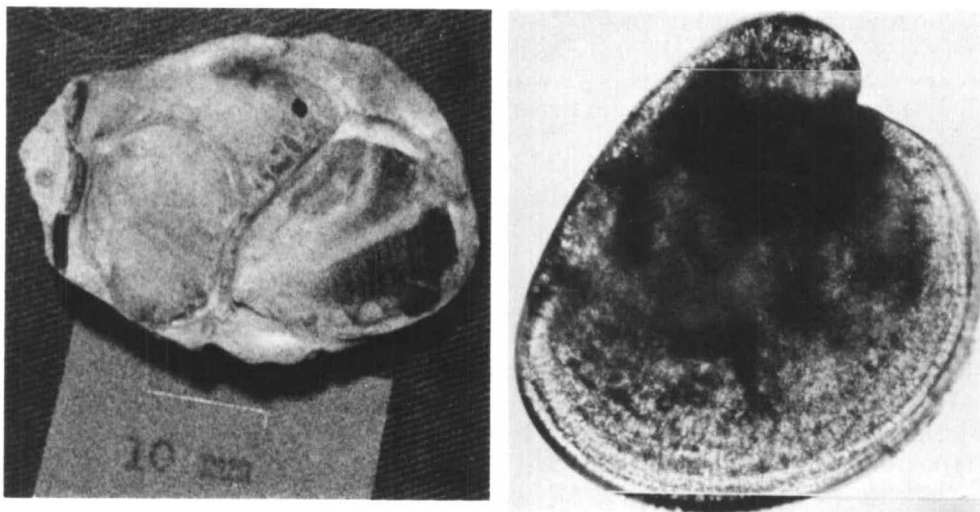
Figure 4. (*Left*) *Crassostrea (O.) brasiliana* Lamarck. 1819. Two smaller specimens are fixed inside a slightly bigger left valve. Type specimens received from Paris Museum and the original label bears the name *Ostrea brasiliana* with the date as 1817 (see text for details). Fig. 4 is by photomacrography using Nikon bellows focusing attachment PB-5.

Figure 5. (*Right*) Prodissoconch of *Crassostrea paraibanensis*; seen with the left valve above and deep umbo near the hinge line. This figure is from color print by photomicrography.

laboratory conditions have shown that they have valves of equal size, a highly extensile cylindrical muscular foot, which is used for crawling and correcting their setting position; usually a siphon protrudes in the center between ventral margins and also byssus threads are seen at this stage. The ventral valve margins are distinctly scalloped in spat of *C. brasiliana* while this feature is absent in *Crassostrea paraibanensis* where the valves are more rounded and their margins smooth.

DISCUSSION

The position of oysters within the class Bivalvia has recently been reviewed by Stenzel (1971), and his classification incorporates palaeontological evidence, including knowledge of the soft parts.

Crassostrea paraibanensis, when fully grown, is large in size and extends, along the mid-axis between the dorsal and ventral ends, to 160 to 250 mm or more in height, and weighing, with shells intact, between 650 and 1,312 g; wet meat weight 56 to 110 g, and dry weight 2.9 to 4.2 g. Very seldom the length of the shell, in anteroposterior axis parallel to the hinge axis, nearly equals the height. The width, maximum distance between the outsides of the closed shells, is due to the thickness of both valves. Occasionally, the right valves grow to greater thickness than the left valves. Usually, the males are more elongated and laterally curved than the females. Often the curvature is towards the posterior margin with the left valve on the bottom.

The thickness of the shell, deeply cupped left valve, presence of an extensive promyal chamber, muscle attachment farther removed from the hinge, oviparity, and typically estuarine habitat all support the view that this oyster should be placed in the genus *Crassostrea* (Sacco, 1897).
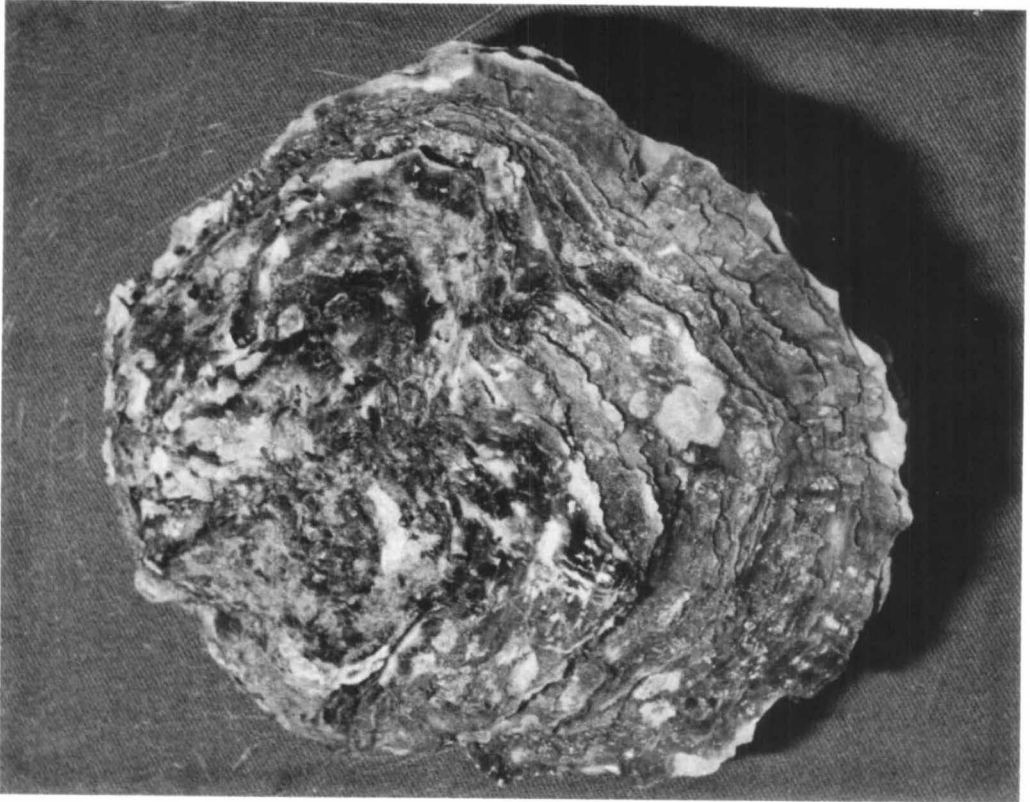
Figure 6. *Crassostrea sp.*, only two specimens were collected from the lagoon Tijuca, Rio de Janeiro, at 2.8 m depth.

The shell characteristics, the form of the beak with deep furrow and with cross ripple marks, the straight hinge, in conjunction with the anatomy of the soft parts, prodissoconch, physiology and ecology of this bivalve, clearly separate *Crassostrea paraibanensis* from the other two species. *C. paraibanensis* appears to be related to the group which includes *Crassostrea brasiliana* and *Crassostrea sp.* (Fig. 6). Furthermore, *C. paraibanensis* and *C. brasiliana* occur side by side in the same estuary; the former occurs on the muddy bottoms at depths between 2 to 3.5 m, while the latter is distributed very widely between the tide marks, thus differing in their ecological habitats. Table 1 compares the three species.

The identification of adult *Crassostrea paraibanensis* is not difficult because it is probably the largest of Brazilian oysters and always found in waters that are well below the low tide mark. The prodissoconch is not easily distinguished but the pediveliger larvae of *Crassostrea paraibanensis* are recognisable on the basis of a deep umbo, well developed velum, long and powerful cilia and their comparatively large size. Ranson's (1948, 1960) idea of classifying adult oysters by their prodissoconchs is difficult because the early larval shell characters are hardly sufficient to separate the species of *Crassostrea*.

The abrupt constriction of the distal part of the intestine to form a tubular rectum, however, is not evident in *Crassostrea brasiliana* where it is a simple continuous tube of uniform diameter, an anatomical difference which seems note-

Table 1. Comparative diagnostic features of three species of *Crassostrea*

Character	C. paraibanensis	C. brasiliana	C. sp.
Size (mm)			
Height	160–250	30–100	100–110
Length	80–120	24–48	90–100
Width	40–90	20–32	40–50
Adult shell characteristics	Large, elongated, very thick, hard, with ventral margin very broad, nonundulating, thin, fairly smooth and brittle.	Small, elongated, foliaceous, strong, with margin straight, smooth and sharp.	Medium sized, oval, moderately thick, strong with margin slightly undulating, somewhat leathery.
External surface, sculpture & color	Coarse. Distinctly formed thin, lamellated eccentric rings; periphery usually dark grey in color, but it gradually changes to pale brown towards umbo-end.	Smooth. Marked with irregular purple stripes.	Coarse. Concentric rings; Mossy grey.
Valves	Unequal.	Unequal.	Nearly equal.
Left valve	Deeply cupped.	Very concave.	Concave.
Right valve	Shallow, tightly fitting.	Flat, well fitting.	Slightly concave, loosely fitting.
Color internal surface	Milky white and glossy.	White with purple margin towards the periphery.	White.
Internal anatomy	Relatively large promyal chamber.	Promyal chamber present.	Promyal chamber somewhat reduced.
Muscle scar	Combination of half-kidney and half-crescent-shaped.	More round.	Oval.
Pigmentation	Deep-brown.	Purple color or rarely faint blue.	Absence of color.
Muscle attachment	Farther removed from the hinge and a little towards venter from the center.	Near the center.	Very little towards dorsum from the center; and the surface of attachment is deeply indented, a feature that easily distinguishes this from the rest.
Hinge axis & resilium	Edentulous, hard, and fairly smooth with longitudinal and transverse striations.	Hard and smooth.	Short and coarse.
Ligament	Covering the hinge but a greater part spreads out externally on the shell.	Covering the hinge and external.	Covering the hinge and reduced.
Beak	Straight, with pronounced furrow that is transversely rippled.	Short, shallow groove.	Very much reduced or almost absent.

Table 1.   Continued

Character	C. paraibanensis	C. brasiliana	C. sp.
Physiological characteristics			
Sex	Separate.	Separate.	Separate.
Size & number of eggs	Small, over 29,000,000 per spawn.	Small, 50,000,000* per spawn.	Unknown.
Spawning	June to August.	Round the year.	Unknown.
Fertilization	External.	External.	Unknown.
Larval development	Outside, oviparous.	Outside, oviparous.	Unknown.
Occurrence	Estuaries at depths 2–3.5 m & on soft muddy bottom.	Estuaries, lagoons between tide marks with very wide distribution.	Estuaries near river mouths at depths of 2–3 m. Prefers high salinity & confined to Rio de Janeiro.

* Mattox (1949)

worthy; the absence of crenulation at each end of the hinge axis of the prodisso-conch and the spat features can also help to separate this species from the others.

Crassostrea paraibanensis also spawns, as far as known, once a year during the winter; no reversal of sex or hermaphroditism has been observed. Hermaphroditism in this group is very rare, but instances where a very small percentage of oysters change their sex after first spawning have been reported (Korringa, 1941; Yonge, 1960; Galtsoff, 1964; Durve, 1965). Adult sculpture is very different from *Crassostrea brasiliana* and *C. sp.* and sexual dimorphism frequently exists.

Although *Crassostrea paraibanensis* is closely related to *Crassostrea angulata* and *Crassostrea virginica*, it differs in many respects from all known species of the genus *Crassostrea*. From a phylogenetic point of view, the relatively large size of *Crassostrea paraibanensis* suggests that it is more likely to have descended from the stock of *Crassostrea gryphoides* of Tethys sea origin, an ancestry which gave rise to all other large brackish-water species (Stenzel, 1971) than from the Pacific ancestors of Miocene Age.

Under the tropical conditions of Brazilian coastal waters, this species is better adapted for wider changes of salinity, temperature, pH, and turbidity.

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